MINIREVIEW

Climate change effects on beneficial plant–microorganism interactions

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Abstract

It is well known that beneficial plant-associated microorganisms may stimulate plant growth and enhance resistance to disease and abiotic stresses. The effects of climate change factors such as elevated CO_2, drought and warming on beneficial plant–microorganism interactions are increasingly being explored. This now makes it possible to test whether some general patterns occur and whether different groups of plant-associated microorganisms respond differently or in the same way to climate change. Here, we review the results of 135 studies investigating the effects of climate change factors on beneficial microorganisms and their interaction with host plants. The majority of studies showed that elevated CO_2 had a positive influence on the abundance of arbuscular and ectomycorrhizal fungi, whereas the effects on plant growth-promoting bacteria and endophytic fungi were more variable. In most cases, plant-associated microorganisms had a beneficial effect on plants under elevated CO_2. The effects of increased temperature on beneficial plant-associated microorganisms were more variable, positive and neutral, and negative effects were equally common and varied considerably with the study system and the temperature range investigated. Moreover, numerous studies indicated that plant growth-promoting microorganisms (both bacteria and fungi) positively affected plants subjected to drought stress. Overall, this review shows that plant-associated microorganisms are an important factor influencing the response of plants to climate change.

Introduction

The global climate is predicted to change drastically over the next century and various parameters will be affected in this changing environment (Houghton *et al.*, 2001). This is the case for atmospheric CO_2 concentrations that increase continuously (IPCC Climate Change, 2007). Additionally, global surface temperatures are predicted to increase between 1.8 and 3.6 °C by the year 2100, driven by increased atmospheric CO_2 levels derived from natural and/or anthropogenic sources (IPCC Climate Change, 2007). Because of increased temperature, soil water content is expected to decrease in some areas (Le Houérou, 1996), leading to enhanced drought in several areas of the world. Therefore, considerable climate changes are currently ongoing. These climate-changing parameters are known to affect terrestrial macroorganisms such as plants. However, recent studies have shown that other organisms and ecosystems may be impacted as well.

Virtually all land plant taxa investigated have well-established symbioses with a large variety of microorganisms (Nicolson, 1967; Brundrett, 2009). Some of them can be neutral or pathogenic for their hosts according to the de Bary definition (de Bary, 1879), whereas others are known to support plant growth and to increase plant tolerance to biotic and abiotic stresses (Bent, 2006). Many of these plant growth-promoting microorganisms colonize the rhizosphere, the portion of soil attached to the root surface and influenced by root exudates and by microorganisms (Bent, 2006; Lugtenberg & Kamilova, 2009). Some microorganisms can also enter the root system of their hosts and enhance their beneficial effects with an endophytic lifestyle (Stone

et al., 2000). This is the case for plant growth-promoting fungi (PGPF) such as arbuscular mycorrhizae, ectomycorrhizae and other endophytic fungi (Das & Varma, 2009), as well as plant growth-promoting rhizobacteria (PGPR – Kloepper & Schroth, 1978) or plant growth-promoting bacteria (PGPB – Bashan & Holguin, 1998).

Altered environmental conditions due to climate change are likely to induce changes in plant physiology and root exudation. Elevated CO_2 in particular will, in many cases, lead to increased C allocation to the root zone and potentially also lead to altered composition of root exudates. Alterations might include changes in the availability of chemoattractants or signal compounds as well as a different C/N ratio or nutrient availability (Kandeler *et al.*, 2006; Haase *et al.*, 2007). Elevated temperature and drought might induce similar changes, and together they are likely to lead to changes in the composition, abundance or activity of plant-associated microbial communities. Climate change may thus substantially impact the diversity and activities of such plant-associated microbial communities (Drigo *et al.*, 2008). Consequently, microorganisms known for their beneficial effects on plant growth or health might also be impaired, in terms of exhibiting their desirable properties and their colonization capacity under certain conditions. However, a detailed understanding on how exactly plant-associated microbial communities are influenced either directly by altered environmental conditions or indirectly by altered plant physiology and how this affects plant performance and finally ecosystem functioning is still missing.

Mycorrhizal fungi and endophytes as well as PGPB are applied as biocontrol agents, biofertilizers and/or phytostimulators in agriculture (Vessey, 2003; Welbaum *et al.*, 2004; Lugtenberg & Kamilova, 2009) or as degrading microorganisms in phytoremediation applications (Denton, 2007). As impacts of global change may affect their performance, a better understanding is thus needed to select appropriate strains performing well under altered conditions. In this paper, we review and discuss the potential impacts of the major environmental parameters likely to be affected by climate change – elevated CO_2 concentrations, warming and drought – on the performance of plant growth-promoting microorganisms, both fungi and bacteria. In this review, we focus on four major groups of plant-associated microorganisms, namely arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (ECM), endophytic fungi and plant growth-promoting root-associated bacteria.

Effect of global changing conditions on AMF

Approximately 90% of plants form mycorrhizal associations (Brundrett, 2009; Smith & Read, 2009), and 60% of these plants establish symbiosis with obligate symbionts such as AMF belonging to the group of PGPF (Fitter & Moyersoen, 1996). AMF are known to enhance plant nutrient uptake (mostly phosphate) or confer other benefits in exchange for rhizosphere carbohydrate compounds (Koide, 1991; Newsham *et al.*, 1995). However, due to climate change effects such as increasing CO_2 concentrations in the atmosphere, soil warming or drought stress, many studies have reported indirect effects of these parameters on these plant-associated fungi (Baon *et al.*, 1994; Sanders *et al.*, 1998; Augé, 2001). An overview of published data can be found in Supporting Information, Table S1 and a scheme on potential effects is depicted in Fig. 1a and b).

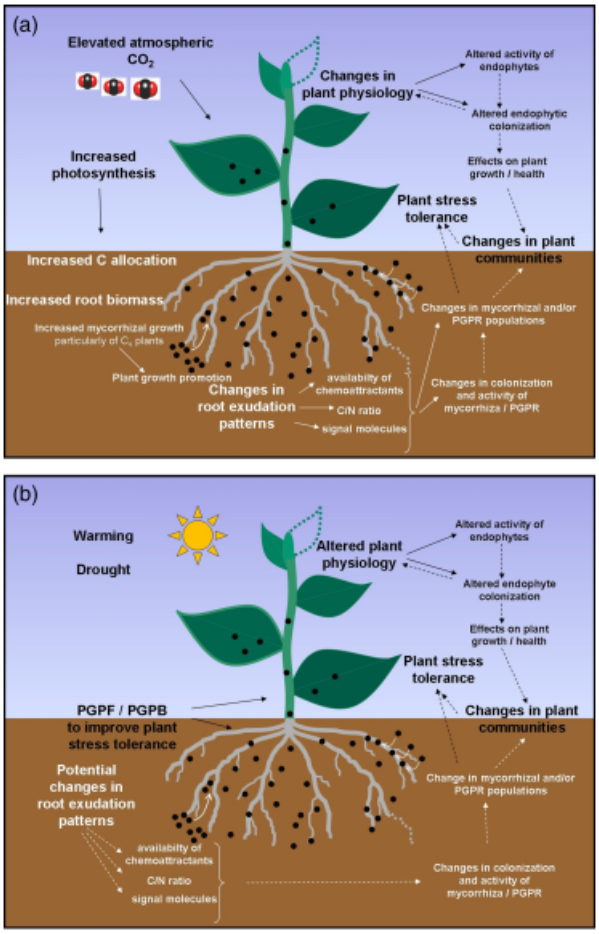

Fig. 1. Potential effects of (a) elevated CO_2 concentrations and (b) warming and drought on beneficial plant–microbe interactions. •, AMF, EcM, fine endophytic PGPF and PGPB; see text for more details.

Effects of elevated CO_2 levels

Increased ambient CO_2 levels were reported to have effects on hyphal growth and root colonization by AMF in the majority of studies (Table S1). For instance, Sanders *et al.* (1998) showed that at 600 $\mu L\,L^{-1}$ of CO_2, external hyphae of

AMF strains show an increased growth in the rhizosphere of *Prunella vulgaris* in comparison with ambient CO_2 ($350\,\mu L\,L^{-1}$), which can be explained by increased C allocation to their external hyphae (Rillig & Allen, 1999). Similarly, internal hyphae of AMF showed the tendency to increase. This might also be due to increased root biomass as a result of increased CO_2 levels (Sanders *et al.*, 1998). Contrasting results on CO_2 effects on plant–AMF association were, however, obtained by Gavito *et al.* (2000), who showed, with *Pisum* sp. as a host plant, that mycorrhizal development of some AMF strains was not affected by CO_2 concentration. Different AMF fungi vary from each other in their effects on host plants, and several studies reported that some AMF have a specific niche in that they preferentially associate with some host plants or occur under specific conditions (e.g. soil type, management, ecosystem type) (Smith & Read, 2009; Verbruggen *et al.*, 2010). Accordingly, distinct mycorrhizal strains, plant genotypes or specific associations might respond differently to altered environmental conditions.

Plant species and plant functional groups respond differently to elevated CO_2. Poorter & Navas (2003) reported that elevated CO_2 levels enhanced aboveground biomass of C_3 plants on average by 45%, whereas C_4 plants showed an increase in their biomass production by only 12%. Differences in plant physiology and carbon allocation patterns inside the plant can at least in part explain these differences. Moreover, these differences may also be interlinked with mycorrhizal colonization levels. AMF colonization of C_4 plants generally increases under elevated CO_2, but for C_3 plants, this seems not to be the case (Monz *et al.*, 1994; Tang *et al.*, 2009). C_4 plants may allocate more carbohydrates to AMF to benefit more from mycorrhizal fungi and may drive the selection of AMF colonizers, while C_3 plants use additional carbon for biomass production. This example demonstrates that environmental conditions altered by elevated CO_2 levels might not only affect plant–microorganism interactions in general, but that they can also change plant competition and plant community structure, partly because of altered plant–microorganism interactions.

The data available so far have indicated that elevated atmospheric CO_2 levels usually enhance the colonization behavior of AMF. As a consequence, this may subsequently increase the plant growth-promoting effects of AMF (Tylianakis *et al.*, 2008), because AMF colonization is known to increase nutrient uptake (Harris & Paul, 1987; Wright *et al.*, 1998; Syvertsen & Graham, 1999; Smith & Read, 2009). Any elevation of CO_2 concentrations may therefore lead to enhanced plant growth promotion in the case of increased AMF abundance. However, in many natural ecosystems, plant growth is limited by nutrient availability (Reich *et al.*, 2006) and not by carbon supply (Körner, 2003). Hence, enhanced levels of CO_2 will not necessarily increase plant productivity under field conditions.

Effects of temperature

Responses of AMF to increased temperature have been investigated (see some examples in Table S1, Fig. 1b). In the majority of cases, increased temperature had a positive impact on AMF colonization and hyphal length. In some cases, however, no effects or negative effects of enhanced temperature on AMF were reported (Table S1). However, the plant itself – without AMF colonization – can respond to soil warming. The extent of plant growth increase or decrease at a certain temperature and at a certain level of increase will depend on the plant species (Heinemeyer & Fitter, 2004). In addition to these effects on plant growth, AMF may respond to higher temperatures with enhanced growth and plant colonization for the majority of strains (Furlan & Fortin, 1973; Graham *et al.*, 1982; Fitter *et al.*, 2000). This was demonstrated for instance with strains of *Glomus intraradices*, *Glomus mossae* as well as with many others (Baon *et al.*, 1994; Monz *et al.*, 1994). Temperature may also significantly alter the structure of the AMF hyphal network and induce a switch from more vesicles (responsible for storage) in cooler soils to more extensive extramycorrhizal hyphal networks (indicating growth) in warmer soils (Hawkes *et al.*, 2008). This may be linked to faster carbon allocation to the rhizosphere and an increased respiration of the extramycorrhizal mycelium at a high soil temperature (Heinemeyer *et al.*, 2006).

Effects of drought

Drought stress might be an additional consequence of global warming. The effects of drought on AMF have been reviewed thoroughly by Augé (2001) (see examples of studies shown in Table S1). Generally, drought reduced AMF colonization (as reviewed by Augé, 2001; Fig. 1b). The kind of the response can be strain-dependent as reported by Davies *et al.* (2002), who demonstrated that drought enhanced arbuscule formation and hyphae development of *Glomus* sp. strain ZAC-19, whereas colonization by a *Glomus fasciculatum* strain was reduced. Several studies showed, furthermore, that different AMF lost the ability to colonize plants internally under drought conditions (Ruiz-Lozano *et al.*, 1995; Schellenbaum *et al.*, 1998; Staddon *et al.*, 2004). However, contrasting results were also obtained (reviewed in Augé, 2001), and may result from specific adaptations of certain AMF strains to drought conditions.

Drought is frequently responsible for reduced plant growth and both roots and aerial plant parts may be impacted. This may lead to changes in the allocation of photosynthates in the rhizosphere as well as in extramycorrhizal mycelium formation. The density of extramycorrhizal

hyphae was not affected by drought as demonstrated with two *Glomus* sp., but more hyphae were produced under drought conditions when expressed relative to root length (Staddon *et al.*, 2004). This may be explained by the fact that part of the mycelium might be dead (Staddon *et al.*, 2003) and that most hyphae could have been produced before drought (Staddon *et al.*, 2004). However, plants may change the type of mycorrhiza colonizing their hosts during longer exposure of drought as it was shown by Querejeta *et al.* (2009). In that study, oaks were colonized by ECM with reduced colonization ability under drought conditions, while AMF were not affected. These findings suggest that oak woodlands in water-limited ecosystems may become increasingly reliant on the AMF symbiosis under future climate change scenarios with enhanced probability of drought, such as predicted for the US southwest and other world regions. Oaks are known to form a tripartite symbiotic association with both AMF and ECM. However, other plants only form associations with either AMF or ECM. As a consequence, McHugh & Gehring (2006) suggested that drought can alter the outcome of competition between AMF shrubs and EMF trees, with the AMF shrubs benefiting during drought. In extreme cases, altered AMF colonization could have extreme effects on plant ecology and consequently could drastically influence ecosystems.

A number of studies reported that AMF can enhance the drought resistance of plants (for a review see Augé, 2001), a feature that may become more important with an expected increased frequency of dry periods in several areas of the world. This is an important characteristic in terms of the ability of plants to cope with altered conditions due to climate change. These beneficial effects were shown with different plant species and have been reported to be responsible for higher root/shoot ratios and increased biomass and yield of various crops (see Al-Karaki & Al-Raddad, 1997; Al-Karaki & Clark, 1998; Al-Karaki *et al.*, 2004). The beneficial association between some strains of AMF and plants may thus reduce the severe effects of water limitation to plants. Moreover, some AMF may resist drought stress better than others. The beneficial effects of specific AMF types have been demonstrated (see examples in Table S1), and plant inoculation with certain types of AMF can thus be promising for food productivity under drought stress conditions.

Ectomycorrhizas and climate change parameter effects

Various plant species, most importantly forest trees, interact with ECM, which, similar to AMF, provide micronutrients to their hosts and allow access to organic nitrogen as well as phosphate, which is then transferred to the host (Smith & Read, 2009; Courty *et al.*, 2010). ECM can also increase seedling survival and establishment (Horton *et al.*, 1999; Dickie *et al.*, 2002) as well as induce several other additional beneficial effects (van der Heijden & Horton, 2009).

Effects of elevated CO_2 levels

Several studies have reported similar responses of ECM and AMF to climate change. As for AMF, it has been shown that increased CO_2 concentrations may induce changes in ECM colonization and/or community structures; however, interactions between ECM and plants are not necessarily impacted (Table S1, Fig. 1a). It has been reported that mycelial biomass production by *Hebeloma crustuliniforme* in *Pinus sylvestris* (L.) Karst. seedlings was significantly greater under elevated CO_2, up to a threefold increase in comparison with ambient CO_2 conditions (Fransson *et al.*, 2005). This suggests that the fungus was able to produce more mycelium as a consequence of increased C availability. Other studies demonstrated similar effects of elevated CO_2; for instance, extramycorrhizal mycelial growth increased under elevated CO_2 levels for *Pinus* seedlings (*P. sylvestris*) inoculated with *Pisolithus arhizus*, *Paxillus involutus* or *Suillus bovinus* (Ineichen *et al.*, 1995; Rouhier & Read, 1998) or for *Pinus echinata* Mills (Norby *et al.*, 1987). The mycorrhizal fungus *Pisolithus tinctorius*, which depended entirely on plant assimilates of *Pinus silvestris* L., grew additionally much faster at increased CO_2 – three times more mycorrhizal root clusters were formed and the extramycorrhizal mycelium produced had twice the biomass at elevated in comparison with that produced at ambient CO_2 levels (Ineichen *et al.*, 1995). Garcia *et al.* (2008) further observed a 14% increase in ECM root colonization with an increase in CO_2, and Runion *et al.* (1997) showed with *Pinus palustris* L. and ECM taxa that increase fine-root length and ectomycorrhizal colonization under elevated CO_2 resulted in higher (almost double) numbers of ECM per seedlings at each sampling site. These studies clearly demonstrated that elevated CO_2 can increase ECM colonization of host plants. This can be highly relevant for the nutrient availability of plants. However, it has also been reported that mycorrhizal formation was only temporarily increased due to elevated CO_2 (O'Neill *et al.*, 1987; Lewis *et al.*, 1994). Furthermore, Markkola *et al.* (1996) showed that fungal biomass in roots and in soil and in particular the fungal types *Cenococcum geophilum* and *Suillus* sp. associated with Scots pine (*P. sylvestris* L.) did not increase under these conditions. Elevated CO_2, moreover, had a negligible effect on mycorrhizal development of *P. tinctorius* associated with *Pinus ponderosa* (Walker *et al.*, 1995a). In parallel, another study with *P. ponderosa* and *P. tinctorius*, subjected to two levels of CO_2, demonstrated no change in colonization after 4 months, but increased colonization at the end (1 year) of the experiment (Walker *et al.*, 1995b). This clearly shows

that the interaction between ECM and plants may be impacted very differently by elevated CO_2 levels. Similar to AMF (Klironomos *et al.*, 1998), genotype-specific responses of ECM colonizing plants grown under elevated CO_2 conditions have been reported (Gorissen & Kuyper, 2000). A recent meta-analysis showed that colonization and ECM root tips generally increased under elevated CO_2 (Cudlin *et al.*, 2007). There is also the potential for plant species-specific effects of increased CO_2 on associated mycorrhizal assemblages (Godbold & Berntson, 1997; Godbold *et al.*, 1997; Fransson *et al.*, 2001). This can potentially affect plant growth promotion. Indeed, the number of species forming extensive extramycorrhizal mycelia and rhizomorphs increased under elevated CO_2 (Rouhier & Read, 1998; Parrent *et al.*, 2006; Courty *et al.*, 2010) and elevated CO_2 may increase ECM occurrence (Tingey *et al.*, 1997). Altered CO_2 concentrations can, moreover, induce a shift in the composition and structure of ECM communities as well as in the abundance of a few species (Rygiewicz *et al.*, 2000; Fransson *et al.*, 2001; Courty *et al.*, 2010; examples can be found in Table S1), potentially leading to effects on plant growth promotion.

Several studies reported that the positive effects of elevated CO_2 on mycorrhiza formation subsequently led to enhanced water and nutrient uptake by the host plants (Norby *et al.*, 1987; Ineichen *et al.*, 1995; Lewis & Strain, 1996; Kytöviita *et al.*, 1999; Loewe *et al.*, 2000; reviewed in Buscot *et al.*, 2000). It is, however, important to note that increased C allocation to ECM does not translate automatically to increased uptake of nutrients and thus to increased forest productivity. A better understanding of how elevated CO_2 impacts fungal species as well as their interaction with their hosts is still required.

Effects of warming

As with elevated CO_2, the effect of temperature on ECM and their hosts has been investigated in several studies (Table S1, Fig. 1b). Respiration of ECM strains of *C. geophilum*, *Suillus intermedius* and *Lactarius* cf. pubescens can be for example reduced under increasing temperature (Malcolm *et al.*, 2008). It has been, moreover, demonstrated that *C. geophilum* morphotypes 12 and 40 have decreased colonization in *Quercus myrsinaefolia* under elevated temperature (Kasai *et al.*, 2000). However, in other studies, soil temperature increased the percentage of total ECM colonization such as in the case of pinyon pine (*Pinus edulis* Engelm.), with soil-type-dependent results (Swaty *et al.*, 1998). Alternatively, Clemmensen *et al.* (2006) showed that the shrub *Betula nana* (dwarf birch) of arctic tundra ecosystems did not show changes in fungal biomass or ECM mycelial production, but warming decreased fine root biomass relative to aboveground biomass in ectomycorrhizal plants, and thus colonization of fine roots by ECM increased slightly. Warming may further affect the ECM morphotypes colonizing the roots of host plants (some reports such as the study of Rygiewicz *et al.*, 2000 are addressed in Table S1). Therefore, not only elevated CO_2 but also increased temperatures may induce changes in ECM communities.

Effects of drought

Drought can significantly impact ECM colonization and community structures (Shi *et al.*, 2002; Swaty *et al.*, 2004). Different ectomycorrhizal taxa responded, however, differently to drought in terms of their patterns of occurrence/abundance (Shi *et al.*, 2002). Drought, moreover, significantly decreased mycorrhizal colonization of Norway spruce trees (Nilsen *et al.*, 1998) or of several Mediterranean shrubs (Lansac & Martin, 1995), *Pinus muricata* (with Rhizopogon sp.; Kennedy & Peay, 2007), *Pinus oaxacana* (Valdés *et al.*, 2006), but not of *Pinus taeda* seedlings (Meier *et al.*, 1990). This demonstrates that ECM colonization of only some plant species is affected by drought. Furthermore, a specific adaptation in colonization by some ECM species seems to occur, which may lead to community shifts under reduced soil water availability.

As some ECM strains confer plant beneficial effects even under drought conditions, they might find application in alleviating drought stress (Parke *et al.*, 1983; Svenson *et al.*, 1991; Morte *et al.*, 2000), for example for reforestation. Symbiosis with *C. geophilum* is stimulated for example under a low water content as this fungus survives better under drought stress than others (Pigott, 1982). Host trees furthermore benefitted after a period of drought (Jany *et al.*, 2003; di Pietro *et al.*, 2007; Courty *et al.*, 2010). To test the effects of drought stress on different ECM fungi, di Pietro *et al.* (2007) developed a simple method that discriminated between two ectomycorrhizal morphotypes associated with beech (*Fagus silvatica*) – *Lactarius subdulcis* and *C. geophilum*. The authors confirmed the ability of the latter fungal species to protect roots against desiccation. Other ECM with the ability to improve plant performance under drought stress can be found in Table S1.

Various mechanisms can explain drought stress acclimatation. Bogeat-Triboulot *et al.* (2004) showed for instance, with *Pinus pinaster* seedlings and *Hebeloma cylindrosporum*, that the fungus improved the water-uptake capacity of the root system. Egerton-Warburton *et al.* (2008) indicated, moreover, that the efflux of hydraulic lift water from the external mycorrhizal mycelia of ECM may be a complementary explanation for plant nutrient acquisition and survival during drought. In parallel, drought-stressed mycorrhizal *Acacia* tolerated water deficiency via tolerance of lower xylem pressure potentials and larger water losses (Osonubi *et al.*, 1991). With *P. tinctorius* in *P. taeda* L., Davies *et al.*

(1996) explained furthermore that increased drought-induced resistance of plants can be attributed to drought-induced colonization by ECM and the ability of plants to maintain high transpiration rates as a result of greater lateral root formation and lower shoot mass. Inoculated plants showed higher CO_2 fixation than nonmycorrhizal plants under drought stress (as demonstrated with *Pseudotsunga menziesii* seedlings and *Rhizopogon vinicolor* strain; Parke *et al.*, 1983). Different mechanisms may thus be responsible for ECM-induced stress tolerance. Improved performance of mycorrhizal seedlings under drought stress conditions may also be linked to better P and K nutrition as well as to a more extensive root system with mycelial strands as demonstrated with *Picea sitchensis* and *P. involutus* (Lehto, 1992). The consequences of drought stress tolerance induced by ECM may in addition affect belowground litter quality and quantity as well as accumulation of organic matter in soils. This was for example demonstrated in arctic ecosystems (Clemmensen *et al.*, 2006). Any drought stress can thus not only affect plant–ECM associations but may also, due to add-on effects, influence ecosystem functioning.

Other endophytic fungi and their performance in interaction with plants with changing environmental conditions

Unlike mycorrhizal fungi that colonize plant roots and grow into the rhizosphere, there are microsymbionts such as certain endophytic fungi that reside entirely within plant tissues and may grow within roots, stems and/or leaves, emerging to sporulate at plant or host-tissue senescence (Sherwood & Carroll, 1974; Carroll, 1988; Bacon & De Battista, 1991). This is for example the case for some strains of the taxa *Atkinsonella*, *Balansia*, *Balansiopsis*, *Echinodothis*, *Epichloë*, *Myriogenospora* (White, 1994), *Parepichloë* (White & Reddy, 1998), *Neotyphodium* (Glenn *et al.*, 1996) as well as many others.

Effects of CO_2

Few studies have explicitly investigated the impact of increased CO_2 levels on endophytic fungi other than AMF and ECM (Table S1; Fig. 1a). The ericoids, dark septate endophytes, but not others, showed increased colonization in ericaceous dwarf shrubs under elevated atmospheric CO_2 concentrations (Olsrud *et al.*, 2010). In the case of *Neotyphodium coenophialum* and its host, tall fescue *Schedonorus phoenix*, endophyte infection was reported to be higher under elevated CO_2 compared with ambient CO_2 (Brosi *et al.*, 2009). In contrast, Marks & Clay (1990) reported that CO_2 enrichment did not alter the interactions between host grasses *Lolium perenne* (a C_3 plant), and purpletop grass, *Tridens flavus* (a C_4 plant), and their endophytic–fungal symbionts, *Acremonium lolii* and *Balansia epichloe*, respectively. Additional examples showing no or positive effects are listed in Table S1.

In the case of *Neotyphodium* sp. and its host plants, colonization is a problematic issue as the fungus produces toxins, which are harmful to ruminants. Within endophyte-infected tillers, elevated CO_2 decreased alkaloid concentrations such as ergovaline and loline (Brosi *et al.*, 2009), and, at the same time, litter C : N increased and acid detergent fiber (ADF) decreased (Brosi *et al.*, 2009). In the interaction between *Neotyphodium lolii* and a perennial ryegrass (*L. perenne*), the concentrations of the pyrrolopyrazine alkaloid peramine depended, however, on the interaction between CO_2 and N fertilization. Peramine concentrations declined with increasing N at ambient CO_2, but remained roughly constant across different N levels at elevated CO_2 (Hunt *et al.*, 2005). Taken together, these results suggest that elevated CO_2 may interact with the plant–fungal symbiosis and may lead to increased endophyte infection frequency, although with lowered toxin production (Brosi *et al.*, 2009). The impact of CO_2 on the host plant and its endosymbionts may additionally change the plant carborhydrate content. This was demonstrated for example with *N. lolii* and a perennial ryegrass (*L. perenne*), where infected plants had significantly higher carbohydrate contents than endophyte-free plants, and the difference was greatest under ambient CO_2 conditions (Hunt *et al.*, 2005). Protein concentrations were also influenced: endophyte-free plants had 40% lower concentrations of soluble protein and chlorophyll content under elevated CO_2 than under ambient CO_2. No CO_2 effect on soluble proteins was observed in endophyte-infected plants, but chlorophyll concentrations were lower in endophyte-free plants in comparison with endophyte-infected plants (Hunt *et al.*, 2005). Other examples of CO_2 effects on grass–endophyte interactions are addressed in Table S1. In conclusion, elevated CO_2 can change the plant physiology of the host grass infected with endophytic fungi, which may impact grazing ruminants. Endophyte-free plants have been required as a solution for herbivores; however, fungal contamination from other plants of natural ecosystem can occur, and moreover, elevated CO_2 may lead to increased occurrence of endophyte infections resulting in overall effects on the ecosystem.

Interestingly, plant–microorganism associations such as those between endophytic fungi and grasses can protect plants against insect herbivores, also under elevated CO_2 conditions. Lepidopteran larvae fed with plant material that was infected with fungal endophytes (*Balansiae*) consumed less material, but were also negatively affected in their growth and survival under elevated CO_2 (Marks & Lincoln, 1996). Increased CO_2 levels may therefore influence infection and damage by insect herbivores, potentially resulting in add-on effects on the whole ecosystem.

Warming and effects on beneficial plant–endophytic fungi associations

It is known that soil warming may impact beneficial associations between plants and fungal endophytes (Table S1; Fig. 1b; Applebee *et al.*, 1999; Newman *et al.*, 2003; Hunt *et al.*, 2005), and temperature appears to be a major parameter affecting fluctuation of endophyte occurrence in plant tissues (Ju *et al.*, 2006). It has been, however, demonstrated that the endophyte infection frequency of *N. coenophialum* of its host tall fescue *S. phoenix* was not impacted by warming. Warming moreover, had no effect on ergovaline concentrations or on ADF, but it increased loline concentrations by 28% (Brosi *et al.*, 2009). Fujimura *et al.* (2008) reported that warming increased the density of different fungal endophyte genotypes within individual root sections of arctic willow (*Salix arctica*) at a tundra site in the Canadian High Arctic. However, it did not affect the composition, richness or evenness of the community. Any elevation in temperature therefore may not be directly linked to changes in endophyte communities. However, plant species diversity may be impacted by warming, potentially leading to effects on endophytic fungal communities.

Drought stress

It is well documented that endophytic fungi confer a competitive advantage to their host plant by enhancing the resistance to environmental stresses (Clay & Holah, 1999). Some endophytes, moreover, can improve plant growth during drought stress exposure (Table S1; Fig. 1b; Elmi & West, 1995; Hesse *et al.*, 2004; Rodriguez *et al.*, 2008) as reported for AMF and ECM. Endophyte infection conferred population stability in tall fescue during drought stress through improved tiller and whole plant survival (West *et al.*, 1988, 1993). Such endophytes have been shown to induce mechanisms of drought avoidance (morphological adaptations), drought tolerance (physiological and biochemical adaptations) and drought recovery in infected grasses (reviewed in Malinowski & Belesky, 2000). These features could be beneficial for plant persistence or for recolonization, especially on sites where water is the growth-limiting factor (Hesse *et al.*, 2004). However, this can be problematic due to the fact that some grasses have been planted as endophyte-free in order to reduce herbivore contamination by endophyte-derived toxins, as described above.

Neotyphodium sp. and Arizona fescue (*Festuca arizonica* Vasey), under low water availability, was correlated with higher net assimilation rates, as well as with the production of less dense leaves and greater leaf area per total plant biomass (Morse *et al.*, 2002). This may explain parts of the mechanisms involved in drought tolerance due to endophytic fungi. In parallel, endophyte-mediated adaptation to drought stress was explained as an avoidance mechanism in the case of *Acremonium coenophialum* Morgan-Jones and Gams associated with tall fescue (*Festuca arundinacea* Shreb), and the endophyte had no effect on leaf osmotic potential and minimal effect on plant water soluble mineral and sugar concentrations (Hill *et al.*, 1996). Other examples are listed in Table S1. It is, however, important to note that the effect of drought stress tolerance differs with plant genotypes and endophyte strains (Hill *et al.*, 1996). White *et al.* (1992) did not show evidence for endophyte-mediated drought tolerance induced by *F. arundinacea* and *N. coenophialum*. However, the results depend on the conditions used and the fungal endophyte may induce greater water retention in the leaf sheath and therefore may better protect the internal growing zone from lethal desiccation (Elbersen & West, 1996).

Environmental conditions of the original habitat of the plants may influence the symbiotic interaction between endophytic fungi and their hosts. Three *L. perenne* L. genotypes collected from different natural habitats were tested in this way for the effects of their fungal endophyte *Neotyphodium* sp. on plant growth and seed yield. In the genotype collected from a dry site, the endophyte infection reduced plant growth at an adequate water supply, but increased regrowth under drought. In the genotype from a periodically either flooded or dry site, endophyte infection significantly promoted the development of reproductive tillers and seed production (effects that are associated with adaptation to drought). In contrast, the genotype that originated from a wet site showed higher sensitivity to drought stress when endophyte infection was present (Hesse *et al.*, 2004). For some host plant genotypes, harboring endophytes can have a metabolic cost under drought stress conditions (Cheplick *et al.*, 2000).

Enhanced osmotic adjustment in the meristematic and growing zone can explain part of the mechanisms involved in drought stress tolerance, allowing survival of tillers by facilitating protection of the apical meristem (Elmi & West, 1995). Upregulation of various genes conferring drought tolerance may also be involved as demonstrated with the model *Pirifomospora indica* and *Arabidopsis thaliana* (Sherameti *et al.*, 2008).

Fungal endophytes can be of great potential for plants in case of severe drought. However, and as cited before, some problems such as in the case of specific endophytes infecting grass can occur. Nevertheless, not only fungal endophytes and their interactions with their host plants may be impacted but other plant-associated microorganisms may also be affected under climate change conditions.

PGPB and climate change conditions

Plants are not only colonized by a wide range of fungi but also by different bacteria (reviewed by Compant *et al.*,

2010), and many of them confer beneficial effects to their hosts (Welbaum *et al.*, 2004; Lugtenberg & Kamilova, 2009). The mechanisms by which bacteria may promote plant growth and health are manyfold and include the production of growth-promoting substances such as hormones, alleviation of biotic and abiotic stresses, pathogen antagonism and induction of systemic responses (reviewed by Lugtenberg & Kamilova, 2009). As plant-associated bacteria depend on root exudates (Rangel-Castro *et al.*, 2005) or plant metabolites (Rasche *et al.*, 2009) and are substantially influenced by environmental parameters due to plant physiological changes (Rasche *et al.*, 2006a, b), it can be expected that environmental conditions associated with climate change will affect these communities. Bacterial endophytic populations, which colonize plant internal tissues such as roots, stems, shoots, leaves as well as flowers, fruits and seeds (Hallmann, 2001; Compant *et al.*, 2005b, 2008, 2010), may be affected in a similar manner. Bacterial endophytes are diverse and adapted to various environments, and may even grow under extreme conditions such as in plants containing high levels of heavy metals (Lodewyckx *et al.*, 2002; Idris *et al.*, 2004). Many of them further have the potential to induce more plant growth-promoting effects than rhizosphere-restricted bacteria (Conn *et al.*, 1997; Hallmann & Berg, 2007), and may mitigate biotic and abiotic stresses via priming of specific plant genes under stress conditions (Hallmann, 2001; Compant *et al.*, 2005a; Hallmann & Berg, 2007).

Effects of elevated CO_2 levels

Elevated CO_2 can impact beneficial bacteria associated with plants. A recent review by Drigo *et al.* (2008) has reported the effects of elevated CO_2 on rhizobacterial communities. In addition to bacterial communities colonizing the rhizosphere, endophytic populations may also be impacted (Table S2; Fig. 1a).

Most information on the effects of elevated ambient CO_2 on plant-associated bacteria has so far been obtained by studies performed within the long-term 'Free Air CO_2 Enrichment (FACE)' experiment performed in Switzerland (Hebeisen *et al.*, 1997). In this experiment, elevated CO_2 triggered the interaction of legumes with rhizobia (Schortemeyer *et al.*, 1996; Marilley *et al.*, 1999; Montealegre *et al.*, 2000), which are well known for their N fixation in association with legumes as well as for their additional plant growth-promoting activities (Sessitsch *et al.*, 2002). Montealegre *et al.* (2000) additionally showed that atmospheric CO_2 enrichment favored some *Rhizobium leguminosarum* strains over others in some plants. Interestingly, the isolates favored by elevated CO_2 produced 17% more nodules on roots than isolates favored by ambient CO_2 concentrations, suggesting that the plant drives the selection of specific microorganisms under variable environmental conditions. Haase *et al.* (2007) recently reported, moreover, that under elevated CO_2 conditions, N tissue concentrations were reduced in common bean and led to the expression of N deficiency symptoms. Increased root exudation and a related stimulation of rhizosphere-microbial growth have been hypothesized as possible explanations for a lower N-nutritional status of plants grown under elevated atmospheric CO_2 concentrations, which can be due to enhanced plant–microbial N competition in the rhizosphere (Haase *et al.*, 2007).

The FACE experiments have revealed not only information on rhizobia but also on other plant-associated, potentially PGPB such as *Pseudomonas* sp. (Marilley *et al.*, 1999), *Actinobacteria* and *Deltaproteobacteria* (Jossi *et al.*, 2006). Drigo *et al.* (2009) reported for instance plant genotype- and soil-specific effects of elevated CO_2 on *Pseudomonas* and *Burkholderia* sp. as well as on antibiotic production genes. This may be explained by different plant responses to elevated CO_2 leading to altered photosynthate allocation in the rhizosphere. However, *Actinomycetes* and *Bacillus* sp., which are also strong antibiotic producers, were not affected. Specific bacteria or bacterial groups seem to respond differently to atmospheric CO_2 enrichment in association with different plants.

In addition to the differential effects reported by Drigo *et al.* (2009), Marilley *et al.* (1999) showed that elevated CO_2 increased the dominance of *Pseudomonas* sp., which are known to include many plant growth-promoting members, associated with rye, whereas with white clover, the abundance of *Rhizobium* sp. was enhanced (Marilley *et al.*, 1999). In other studies, the proportion of HCN-producing *Pseudomonas* strains, considered as potential inhibitors of root parasitic fungi isolated from bulk and rhizosphere soil and from root fractions of two perennial grassland systems (*L. perenne* and *Medicago coerulea*), was reduced under elevated CO_2 conditions (Tarnawski & Aragno, 2006). However, the proportion of siderophore producers and nitrate-dissimilating strains increased. This is an example indicating that increased atmospheric CO_2 levels might have differential impacts on plant beneficial bacteria, which might have further implications on their application in agriculture or phytoremediation. In the case of elevated CO_2 concentrations, different inoculant strains for application in agriculture will possibly have to be selected because of the distinct performances of plant growth-promoting strains under ambient and elevated CO_2 conditions. Kohler *et al.* (2009) recently reported that a plant growth-promoting *Pseudomonas mendocina* strain enhanced the growth of lettuce plants under elevated CO_2 conditions. Two levels of watering and two levels of atmospheric CO_2 were applied to ascertain the effects observed on plant physiological parameters. Inoculation with the *P. mendocina* strain induced the

highest plant biomass production under all assayed treatments as well as the highest foliar potassium concentration and leaf relative water content under conditions of elevated CO_2 and drought (del Mar Alguacil *et al.*, 2009; Kohler *et al.*, 2009). This demonstrates the potential of PGPB to be used for the alleviation of novel and atypical stresses possibly imposed by climate change, which can be relevant for the future under increasing CO_2 concentrations.

Effects of temperature

Some rhizosphere bacteria and endophytes have been shown to alleviate temperature stress on plants, and these strains may induce growth promotion of different crops at different climates, soils and temperatures (Table S2, Fig. 1b; Bilal *et al.*, 1993; Javed & Arshad, 1997; Bashan & Holguin, 1998). Egamberdiyeva & Höflich (2003) reported, however, that temperature and soil type may affect the performance of plant-beneficial bacteria. *Mycobacterium* sp. 44, a *Pseudomonas fluorescens* and a *Pantoea agglomerans* strain isolated from a semi-continental climate were found to significantly increase the root and shoot growth of winter wheat at 16 °C compared with that at 26 °C in loamy sand. However, *Mycobacterium phlei* strain MbP18 as well as *Mycoplana bullata* MpB46 (all from a semi-arid climate) performed well under both conditions, indicating genotype-specific preferences for certain environmental conditions. This should be taken into consideration for the future selection of bacterial inoculants to improve plant performance.

Some strains of PGPB can grow better at a high temperature than at a low temperature and could be of special interest for application in agriculture exposed to increased temperatures. In an early study, Waldon *et al.* (1989) clearly showed that rhizobia isolated from nodules of the desert woody legume *Prosopis glandulosa* grew better at 36 °C than at 26 °C. These strains were physiologically, however, distinct from other strains belonging to the same species, suggesting that highly adapted strains have evolved. In addition, bacteria colonizing distinct sites may react differently to certain environmental conditions. A study with the endophyte *Burkholderia phytofirmans* strain PsJN demonstrated that a temperature increase from 10 to 30 °C reduced the colonization of this strain in the tomato rhizosphere, whereas endophytic abundance was not affected (Pillay & Nowak, 1997).

After successful colonization, rhizosphere as well as endophytic bacteria may alleviate temperature or drought stress on plants (Aroca & Ruiz-Lozano, 2009) by inducing a systemic response (Yang *et al.*, 2009). This demonstrates the potential role of certain strains for use in agriculture, but by also taking into account the effects of changing conditions on their colonization as well as on their plant growth-promoting capacities.

Effects of drought

The effects of drought on PGPB are summarized in Table S2 and Fig. 1b. As early as 1985, Okon (1985) reported that inoculation with *Azospirillum* strains can improve plant–water relationships and may lead to higher grain yield. Wheat, maize and sorghum seedlings inoculated with *Azospirillum* strains and exposed to water stress, moreover, showed a better water status than control plants, and higher yields under drought conditions were obtained (Sarig *et al.*, 1988; Creus *et al.*, 1998, 2004). In addition, in a non-nourished hydroponic experiment, inoculation of wheat with *Azospirillum brasilense* strain 245 alleviated water stress and the rate of coleoptile growth increased (Creus *et al.*, 1998). Experiments with *A. brasilense* mutants harboring a plasmid encoding trehalose biosynthesis genes were further performed and confirmed that the production of this osmoprotectant can protect plants from osmotic stress (Rodríguez-Salazar *et al.*, 2009). Plants inoculated with the engineered strain, moreover, showed substantially more biomass than control plants (treated with the wild-type strain), suggesting not only that trehalose production is important for mediating drought tolerance but also that genetically engineered microbial inoculants may be used to enhance yield and drought stress tolerance (Rodríguez-Salazar *et al.*, 2009).

In addition to *Azospirillum*, other bacterial genera have been shown to alleviate drought stress by using alternative mechanisms to trehalose accumulation. *Burkholderia phytofirmans* strain PsJN was reported to show beneficial effects on potato and vegetable plants such as for instance some *Cucurbitaceae* under drought stress (Nowak *et al.*, 1995). Furthermore, various *Paenibacillus polymyxa* endophytic strains protected *A. thaliana* against water deficiency (Timmusk & Wagner, 1999). Endophytic bacteria belonging to the *Actinobacteria* have additionally shown the potential to increase plant resistance to drought. The improved tolerance was associated with a higher osmotic pressure of plant cells, accelerated callose accumulation and cell wall lignification of sieve cells (Hasegawa *et al.*, 2004, 2005).

As a result of drought stress, plant-associated communities may change. Recently, different subpopulations of endophytic bacteria colonizing sunflower cultivated under drought conditions or under irrigation management were identified (Forchetti *et al.*, 2007). In particular, one *Achromobacter* strain was found only under drought conditions, indicating a better adaptation to drought stress conditions. Interestingly, endophytic bacteria isolated from sunflower cultivated under drought, compared with plants cultivated with irrigation, indicated a higher plant growth promotion potential (Forchetti *et al.*, 2007).

PGPB may, under drought, induce several responses in plants, which include increased cellular division in roots and

root hairs, decreased distance between the root tip and the root hairs and an increased number of root hairs as reviewed by Michiels *et al.* (1989). This further leads to enhanced water and nutrient uptake by plant roots, especially from deeper soil layers. In addition, the reduction of oxidative stress is correlated with drought stress tolerance induced by plant-beneficial bacteria (Aroca & Ruiz-Lozano, 2009). Under drought conditions, PGPB may furthermore regulate the levels of stress-related hormones, i.e. abscisic acid and ethylene, potentially leading to better plant drought tolerance (Aroca & Ruiz-Lozano, 2009). During drought, ethylene production is in fact known to be enhanced. However, ethylene synthesis may be inhibited by reducing the levels of the precursor 1-aminocyclopropane-1-carboxylate (ACC) by the action of the microbial enzyme ACC deaminase (Glick, 2005). In the last few years, it has become evident, moreover, that some plant-associated bacteria elicit a plant response and thereby induce systemic tolerance (Yang *et al.*, 2009). Plant-associated bacteria, and endophytes in particular, may confer increased osmotic (and likely also drought) stress tolerance via modulating gene expression. However, a detailed understanding of how microorganisms influence plant gene regulation and how altered environmental conditions due to climate change affect this interaction is still lacking.

Conclusions and future prospects

This review shows that climate change affects plant-beneficial microorganisms in many ways, the effects being dependent on the climate change factor studied, plant species, ecosystem type, soil type and microbial genotype. Climate change may affect all types of beneficial plant–microorganism interactions.

The majority of studies performed so far have indicated that elevated CO_2 conditions will lead to increased colonization of PGPF. This is generally in agreement with meta-analyses performed by Treseder (2004) and by Alberton *et al.* (2005), who reported positive plant and mycorrhizal responses to elevated CO_2. The latter authors also discussed that the choice of parameters indicative for fungal growth is highly important, particularly for being able to separate mycocentric and phytocentric views, as already advocated by Fitter (2001). However, we did not distinguish between both views and would like to draw only a general conclusion. It is also important to note that elevated CO_2 concentrations may induce AMF community composition changes (Klironomos *et al.*, 2005). The response of elevated CO_2, but also of warming and drought, will therefore also depend on the plant and the microbial genotype.

The effects of elevated CO_2 on PGPB were more variable, and no general trend in terms of increased or decreased abundance of PGPB has been observed so far (Table S2). Generally, the symbiotic interaction between legumes and rhizobia was enhanced. However, several studies showed that elevated CO_2 may induce changes in the community composition of plant-associated microorganisms also affecting plant-beneficial community members. The response to warming in the published literature was also described. The interaction with plant growth-promoting microorganisms was either enhanced or negatively impacted and seems to depend on the adaptation of microbial and plant genotypes to certain temperatures. Drought generally had the tendency to decrease the colonization of plant-beneficial microorganisms, but many studies showed that inoculation with selected bacteria or fungi reduced drought stress and improved plant performance.

It has been shown that the composition of microbial communities correlates with plant physiology and is likely to be driven by root exudation or metabolite patterns. This indicates that the colonization of plant-associated microorganisms depends on the availability of certain compounds produced by the plant acting as the primary nutrient source, as chemoattractants or signal molecules. Consequently, at elevated CO_2 concentrations, in particular, but also under conditions of increased temperature or drought, different genotypes of PGPF or PGPB, potentially also showing different functional activities, might establish in the plant environment (Waldon *et al.*, 1989; Marilley *et al.*, 1999; Drigo *et al.*, 2009). However, as a result of altered community structures, beneficial microorganisms might have to compete with a different microbial communities and therefore might show an altered colonization behavior. In addition to the potential effects of climate change on microbial colonization characteristics, microbial activities may be affected (Kandeler *et al.*, 2006; Haase *et al.*, 2008). Microbial communities showing different activities or producing altered signals may, in the long term, either result in the establishment of altered communities and/or in the elicitation of different plant responses.

Because of plant genotype-specific responses to elevated CO_2, but also to increasing temperature or drought, climate change will, in the long term, alter plant ecosystems. Plant diversity levels have been reported to have a far more pronounced effect than elevated CO_2 on belowground diversity (Grüter *et al.*, 2006), indicating that short-term studies might considerably underestimate the long-term effects of climate change on beneficial plant–microorganism interactions. Considering the fact that plant-beneficial microorganisms such as mycorrhizal fungi and nitrogen-fixing bacteria provide up to 80% N and up to 75% P and that an extremely high number of plant species are completely dependent on microbial symbionts for growth and survival (reviewed by van der Heijden *et al.*, 2008), it is evident that alterations in the plant-beneficial microbial communities may ultimately influence plant diversity and the diversity

and functioning of the soil microbiota. Furthermore, the abundance or the activity of microorganisms with biocontrol activities may be altered and thereby plant pathogen populations may be affected.

Climate change will induce adaptation processes in plants and microorganisms and might require the selection of adapted plant cultivars in agriculture. However, adaptation processes or the use of cultivars not fully adapted to new environmental conditions could be supported by making use of the plant growth-promotion potential of PGPF/B. Particularly under elevated CO_2 conditions, nutrients such as N might be limiting, leading to the need for enhanced fertilizer input in agriculture. Plant growth-promoting microorganisms supporting nutrient acquisition such as mycorrhizae or N-fixing bacteria may thus gain increasing importance.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Examples of the effects of climate change on the interaction of PGPF with plants.
Table S2. Overview on the effects of climate change on the interaction of plant growth-promoting bacteria with plants.

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